

## Ecology of sexual dimorphism in spiders of the genus *Metepeira* (Araneae: Araneidae)

William H. PIEL

Museum of Comparative Zoology, Harvard University, Cambridge MA 02138, USA.

**Ecology of sexual dimorphism in spiders of the genus *Metepeira* (Araneae: Araneidae).** - Spiders of the genus *Metepeira* living in different habitats show inter- and intraspecific variation in degree of female aggregation. I examined sexual size dimorphism in three species of *Metepeira* in Mexico to evaluate the relationship between habitat, female aggregation, and size dimorphism. *Metepeira incrassata* lives in highly productive habitats, has almost exclusively communal females, and shows little dimorphism. In contrast, *Metepeira* species A lives in less productive habitats, has mostly solitary females, and shows a high degree of dimorphism, with males much smaller than females. Finally, *Metepeira spinipes* shows geographic variation in both female communality and sexual dimorphism. In productive habitats that promote communal females, large males predominate. In less productive habitats that promote solitary females, dwarf males predominate. In habitats that promote a mixture of colonial and solitary females, both dwarf and large males coexist. Large males appear to be adapted for competing against other males in large colonies, whereas dwarf males are adapted for traveling over land in search of solitary females.

**Key-words:** Sexual size dimorphism - colonial behavior - ecology - *Metepeira* - spiders.

### INTRODUCTION

Many spider species show sexual dimorphism, with females larger than males (VOLLRATH 1980). Dimorphism is generally more pronounced among spiders with high male mortality which comes from the risky behavior of searching for widely spaced females (VOLLRATH & PARKER 1992). In the present study, I examined sexual dimorphism in *Metepeira* F. O. Pickard-Cambridge that vary in degree of female aggregation.

Spiders of the genus *Metepeira* living in different habitats show variation in female aggregation (UETZ 1982). *Metepeira incrassata* Pick.-Cambr. occurs in tropical rain forests and 99% of females live in colonies with two or more individuals (UETZ 1988). In contrast, species A (species description in preparation) occur in desert mesquite grasslands and almost 80% of females live solitarily, with group size rarely exceeding ten individuals (UETZ *et al.* 1982). Finally, *Metepeira spiiipes* Pick.-Cambr. is variable in both habitat and sociality. *M. spiiipes* can be found in dry mesquite desert where females are almost entirely solitary, as well as more humid agricultural land around Mexico City where almost 70% live communally (UETZ *et al.* 1982). UETZ (1988) concluded that females aggregate into foraging flocks as a risk sensitive response to prey availability.

In the present study, I examined sexual size dimorphism in species A, *M. incrassata*, and *M. spiiipes* to evaluate the adaptive significance of inter- and intra-specific variation.

## METHODS

I collected specimens of the three *Metepeira* species, species A, *M. incrassata*, and *M. spiiipes*, at 17 different sites in Mexico. I also examined specimens representing about 60 different sites, from the collections of the American Museum of Natural History, the Californian Academy of Sciences, and the Museum of Comparative Zoology.

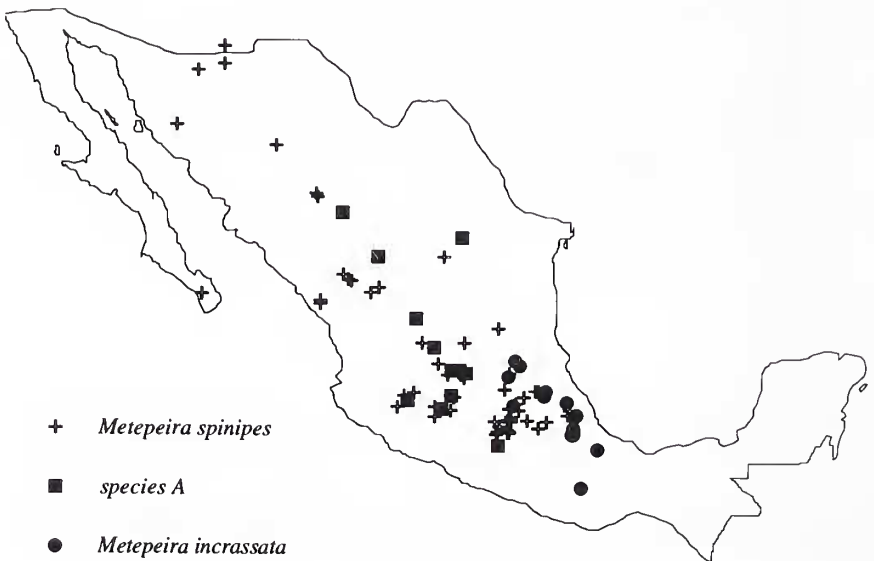


FIG. 1

Geographic distribution of three *Metepeira* species: *M. incrassata*, species A, and *M. spiiipes*, in Mexico.

In my field collections, I used a Sony Pyxis GPS to determine the precise geographic coordinates and altitude of each collection site. For museum specimens, I determined the site coordinates using a USBGN Gazetteer, and site altitudes by consulting a DMAAC ONC J-24 aeronautical map.

For each specimen, I measured body length from anterior tip of the prosoma to posterior tip of the abdomen, using a dissecting microscope equipped with a reticule. For species A and *M. atascadero*, I calculated size-ratio as the body length of each male divided by the average length of all measured females of the same species. For *M. spinipes*, which showed geographic variation in female size, I calculated size-ratio as the body length of each male divided by the average female length for his locality.

## RESULTS

The three species of *Metepeira* differ in their geographic distribution (Fig. 1). Species A occurs in Central Mexico, and *M. incrassata* in southern Veracruz. *M. spinipes* has a wide distribution between California and Mexico City (Fig. 1).

*M. incrassata* shows relatively little sexual dimorphism whereas species A shows a large degree of sexual dimorphism, with 25% of males being less than half the size of the average female (Fig. 2). *M. spinipes* displays a wide range of dimorphism, spanning those of *M. incrassata* and species A (Fig. 2). Male size in *M. spinipes* is remarkably variable. For example, in the town of Huitzilac, I found tiny *M. spinipes* males (4.2 mm) as well as large males (8.5 mm) competing for the same females (9-11

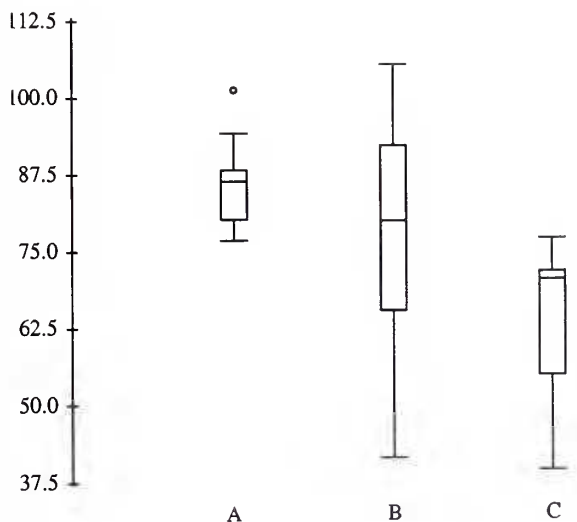


FIG. 2

Box plots of percent male size relative to average female size. A *Metepeira incrassata* (n = 21); B *Metepeira spinipes* (n = 55); C species A (n = 12).

TABLE 1

Lengths (mm) of female and male *M. incrassata*, *M. spinipes*, and Species A. Mean, maximum, and minimum values for females are: *M. incrassata*, 7.57 mm, 9.05, and 6.35 respectively; *M. spinipes*, 9.05 mm, 12.4, and 5.5; Species A, 7.92 mm, 6.0, and 9.5. Sexual size dimorphism expressed as a percent male size relative to mean female size is presented in Fig. 2.

<i>M. incrassata</i> (mm)		<i>M. spinipes</i> (mm)				Species A (mm)	
Female	Male	Female		Male		Female	Male
6.35	6.2	7.9	6.5	7.9	6.25	8.25	3.6
7	6.1	10.75	10	6.75	8.5	8.75	6.25
7.4	5.5	8.3	6.75	8.5	8.95	9.5	6.25
7	6.75	11.75	8.75	7.65	3	8.25	4.1
7.25	6.25	10.75	9.25	7.7	4.5	9.5	5.65
8.2	7.25	9.2	10.6	6.5	8	7.25	6.85
7.35	4.25	10	10.5	6.15	6	6	6.8
6.65	5.75	8.25	9.8	4.75	6.5	7.25	6.5
7.75	5.65	6.75	6.75	4.65	5.1	9.35	6.25
8.85	6.2	9.75	11.5	3.5	8.5	7.5	3.5
8.75	5.75	7.75	7.65	6.3	6.25	6.9	5.75
7	6.4	7.35	9	8.9	7.15	6.5	6.85
6.9	6.75	6.9	7.75	6.75	8.35		
7.35	6.75	7.2	5.5	5	5.6		
7.3	5.25	7.75	8.5	3.75	6		
8.5	7.5	10	7	10.75	9.5		
8.5	8	12	9	3.15	8.25		
8.7	6.6	12.15	11.5	3.75	6.15		
7.15	6.5	8.7	10.5	4.5	9.15		
7.1	6.25	9.15	7.5	5.3	6.5		
7.3	4.6	9.5	8.3	6.5	6.5		
7	6.2	8.5	11	5.5	8.35		
7.8		12.4	8	7.2	6.65		
8		8.8	11	4.75	7.6		
7.3		9	8.25	6.2	7.15		
7.65		8.05	10.4	7	7.7		
9.05		7.1	9.3	8.75	8.5		
7		11.5		4.25			
8.1							
7.25							
7							

mm). In fact, the smallest male *M. spinipes* I examined is only 3 mm in length, the largest 10.8 mm. Examining the effect of altitude and latitude in *M. spinipes* (Fig. 3), there appear to be three distinct regions: low altitude and low latitude localities are dominated by giant males in putatively highly social populations; high altitude and high latitudes produce dwarf males in populations of mostly solitary spiders; and high altitude, low latitude sites have a mixture of large, dwarf, and average sized males in presumably semi-communal populations. These data suggest that males engage in separate, specific strategies because the variance of sexual dimorphism in average

TABLE 2

Lengths of individual *Metepeira spinipes* males and mean lengths of *M. spinipes* females for each locality. Columns are locality (LOC) in latitude and longitude; mean lengths (mm) for all females measured from that locality (MFL); and lengths (mm) of individual males measured from that locality (LIM). Data presented in Fig. 3 are expressed as a percentage of each LIM to its corresponding MFL.

LOC	MFL (mm)	LIM (mm)					
18°50'N 99°41'W	8.5	8					
18°55'N 99°15'W	9.8	8.9					
19°0'N 99°15'W	9.9	7.6	7.2	7.7			
19°2'N 99°16'W	11.3	8.5	4.3				
19°8'N 99°42'W	11	6.2					
19°18'N 99°17'W	9.1	9					
19°20'N 98°35'W	9.5	8.5					
19°22'N 99°16'W	9	6.5					
19°23'N 99°11'W	11.5	7.2	8.4				
19°25'N 99°10'W	9.2	7.7	6.2				
19°25'N 99°10'W	9.2	7.2	6.5	4.8	4.7	6.5	8.4
19°27'N 99°10'W	11.5	5.1	6.3	8.5			
19°32'N 97°9'W	8.8	6.5					
19°42'N 101°16'W	11.5	8.8					
19°41'N 98°52'W	8.7	6.8					
19°43'N 99°13'W	10.3	6.2					
20°7'N 98°44'W	9.3	4.8					
20°10'N 102°53'W	10	10.8					
20°19'N 98°20'W	8.2	3.5	6.3				
20°52'N 100°56'W	6.8	7	6.7				
21°13'N 101°43'W	9	8.5					
21°57'N 102°17'W	7.7	6.3					
23°22'N 105°32'W	6.6	3	4.5				
24°2'N 104°54'W	6.8	3.2	3.8				
24°11'N 105°2'W	8.8	4.5					
24°47'N 101°31'W	8.1	5					
28°24'N 107°26'W	6.5	3.8					

habitats is almost as great as all habitats put together. Indeed, the area in the vicinity of Mexico City (19°-21° North; 2200-2600 meters high) includes males that range from 0.38 to 0.99 of the female's size; all localities, including the dry desert land in Sonora, have males of only marginally greater range -- 0.38 to 1.08 of the female's size.

## DISCUSSION

Many hypotheses have been advanced to explain male dwarfism. FABER (1994) reports that some male jumping spiders in the species *Zygoballus rufipes* mature at an earlier instar, in an attempt to avoid competition with larger males that mature later in the season. The theory of evolution of senescence also explains male dwarfism. It

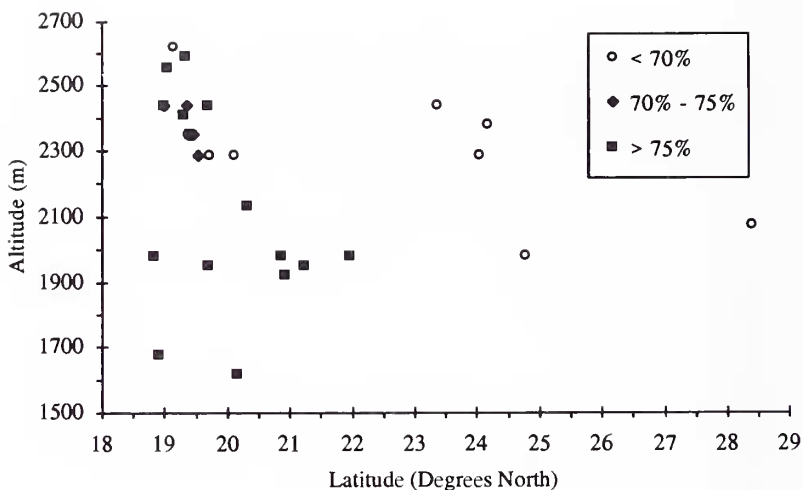


FIG. 3

*Metepeira spinipes*. Percent male size relative to average female size for each locality, plotted against altitude and latitude.

predicts that males that suffer higher mortality rates should undergo more rapid senescence following maturation (WILLIAMS 1957). A restricted adult life-span would increase selection for a shorter maturation time, thus leading to dwarfism.

The results of this study are consistent with the observation that sexual size dimorphism is greater under conditions of high male mortality (VOLLRATH & PARKER 1992) and suggest that variability in sexual dimorphism is a response to variability in communal behavior across lush and harsh environments. Males that live with females in large colonies, as in the case of *M. incrassata*, are unlikely to suffer relatively heavy losses due to predation and accidental death. Males that are forced to travel large distances in search of widely dispersed females, such as species A, will suffer far greater losses than their sedentary siblings. Consequently, one observes a higher degree of sexual size dimorphism in species A than in *M. incrassata* (Fig. 2).

VOLLRATH & PARKER (1992) further argue that higher adult male mortality reduces male intrasexual competition and thereby attenuates the competitive advantage of larger size. Males thus relieved of strong selection for larger size can decrease their chances of juvenile mortality by maturing earlier and undergoing fewer molts, thereby leading to dwarfism (VOLLRATH & PARKER 1992). On the other hand, MAIN (1990) argues that small male mygalomorph spiders are better designed to avoid hazards, such as drought or starvation, and thus would be favored in harsh environments with well dispersed females. Larger males may be more susceptible to predators and less efficient at traveling over land (Bristowe, 1941). Perhaps smaller males are better able to pull themselves along fine airborne threads when passing from one shrub to another.

If the operational adult sex ratio for a given habitat is the primary cause of selection for male size, then one might expect average habitats, hosting semi-communal populations with less skewed sex ratios, to produce males of intermediate dimorphism. Because *M. spinipes* is distributed across a wide range of habitats, this hypothesis was tested. In fact, these average habitats have a wide range of different size males (Fig. 3), suggesting that variation in male size could be the result of two specific and separate strategies: large males competing with other males in colonies; and dwarf males, adapted for cross-country travel, searching for solitary females.

Nonetheless, these results are not inconsistent with the approach of Vollrath and Parker, and it is likely that male dwarfism is in fact a combination of reduced intrasexual competition and specialization for locating dispersed females in harsh environments.

#### ACKNOWLEDGMENTS

I thank H. W. Levi, E. O. Wilson, and N. E. Pierce for providing advice and equipment; T. M. Perez and her family for their hospitality; J. K. Wetterer for his extensive comments; and the George Putnam Research Fund for financial support.

#### REFERENCES

- BRISTOWE, W. S. 1941. The comety of spiders. Vol. II. *Ray Society, London*, (128): 229-560.
- FABER, D. B. 1994. Prizibram's rule and male body-size dimorphism in *Zygoballus rufipes* (Araneae: Salticidae). *Journal of Zoology (London)* 232: 191-198.
- MAIN, B. Y. 1990. Dwarf males in mygalomorph spiders: adaptation to environmental hazards. *Acta Zoolica Fennica* 190: 273-278.
- UETZ, G. W. 1988. Group foraging in colonial web-building spiders. Evidence for risk-sensitivity. *Behavioral Ecology and Sociobiology* 22: 265-270.
- UETZ, G. W., T. C. KANE & G. E. STRATTON. 1982. Variation in the social grouping tendency of a communal web-building spider. *Science* 217: 547-549.
- VOLLRATH, F. 1980. Why are some spider males small? A discussion including observations on *Nephila clavipes*. *Proceedings of the 8th International Congress of Arachnology, Vienna*, 165-169.
- VOLLRATH, F. & G. A. PARKER. 1992. Sexual dimorphism and distorted sex ratios in spiders. *Nature* 360: 156-159.
- WILLIAMS, G. C. 1957. Pleiotropy, natural selection, and the evolution of senescence. *Evolution* 11: 398-411.